Food-Preference of the Nudibranch *Aeolidia papillosa*, and the Effect of the Defenses of the Prey on Predation

BY

VIRGINIA L. WATERS

Pacific Marine Station, Dillon Beach, California 94929

(5 Text figures)

INTRODUCTION

It has long been known that at least European *Aeolidia papillosa* (Linnaeus, 1761) preys on anemones (Boutan, 1898; Eliot, 1910), and more recent observations have confirmed this (Miller, 1961; Swennen, 1961). However, there is little agreement as to which species are eaten or preferred (Table 1). It appears that *Aeolidia* may show a distinct preference within a particular locality, but that the species preferred may vary from place to place.

Of several factors which may cause the nudibranchs to feed on different species in different localities, I was particularly interested in the defense of the prey. There has been little work published on the effect of defenses on predation. Robson (1961) noticed that *Aeolidia* fed only on the base and column of *Stomphia coccinea.* The nudibranchs withdrew whenever they touched the tentacles. Not only were the tentacles effective in limiting predation, but the anemones swam away when *Aeolidia* contacted them, usually leaving the nudibranchs behind. Boutan (1898) briefly discussed the difficulties nematocysts caused *Aeolidia.* He noticed that the nudibranchs secreted large amounts of mucus upon contact with the anemones and that the nematocysts became entangled in this and so did not injure the nudibranchs. Russell (1942) stated that acontia of *Metridium marginatum* became caught in the large quantity of mucus secreted by the nudibranchs but that they were eaten along with the whole anemone. Wolter (1967) described the extrusion of acontia and contraction of *Metridium senile* as *Aeolidia* began to feed on the anemones, with no mention of the effect of such behavior on the nudibranchs. Rosin (1969) found that when *Anthopleura nigrescens* was attacked by the eolid *Herviella* spec. nov. the anemones regularly detached from the substrate within a few minutes. The nudibranchs would hold on to an anemone for a while, but eventually the animals would separate and the anemone would fall. The nudibranchs would then resume feeding on a new anemone.

The relationship between *Metridium senile* and *Aeolidia* is particularly interesting. Nearly all of the European workers and Russell (1942) in New England (Table 1) indicated that *Aeolidia* eats this species or even prefers it to others. No one has said that *Aeolidia* does not eat *Metridium.* However, observing animals from Puget Sound, Washington, I discovered that when I placed a nudibranch on such an anemone, the anemone immediately contracted and extruded acontia. The nudibranch for its part withdrew violently and became covered with thick mucus when touched to the anemone. When placed at the base of an *Epiactis prolifera,* it immediately began feeding. Yet, the acontia of European and New England *Metridium* did not seem to prevent the nudibranchs from attacking the anemones.

In addition to nematocysts, escape responses, and detachment, the occurrence of anemones in dense concentrations of individuals could minimize the effects of predation by reducing the chances that a given individual would be entirely consumed. The adaptive significance of the occurrence of the local *Anthopleura elegantissima* in dense groups could thus be related to predation by nudibranchs. The effectiveness of grouping would depend on the predatory methods of *Aeolidia,* however. In addition to grouping, the column of this anemone is covered with sand so that very little of the body surface is exposed. When the anemones are expanded, the tentacles and oral disk are the most accessible parts.

The primary objectives of this study were (1) to obtain preliminary information on the food of *Aeolidia papillosa*

[1] Present address: P. O. Box 103, Arcata, California 95521

Table 1

Species eaten or preferred by *Aeolidia* (from literature) [2]

Worker	Species preferred	Other species offered or mentioned
McMillan, 1942	not stated	*Tealia crassicornis*
Russell, 1942	not stated	*Metridium marginatum*
Stehouwer, 1952	*Metridium senile*	*Actinothoe anguicoma* *Diadumene cincta* *Tealia felina*
Braams & Geelen, 1953	*Actinia equina*	*Metridium senile* 6 species of hydroids, including *Tubularia indivisa*
Miller, 1961	*Actinia equina*	*Anemonia sulcata* *Sagartia troglodytes* *Tealia felina* *Tubularia indivisa*
Robson, 1961	*Stomphia coccinea*	*Metridium (senile?)* *Sagartia (troglodytes?)* *Tealia (felina?)*
Swennen, 1961	*Actinia equina*	*Metridium senile* *Tealia felina* *Actinothoe anguicoma* *Diadumene cincta* *Sagartia troglodytes*
Wolter, 1967	*Metridium senile*	*Actinia equina* *Sagartia troglodytes* *Tealia felina*

[2] The observations were made in different localities in Europe, except those of Russell, 1942, which were made on the Atlantic coast of the United States

in yet a different part of its range, and (2) to begin to answer the question "What governs local food preference?" by investigating the defensive responses of the prey. The effects of the following potential defenses on predation were studied: (a) nematocysts, particularly those of the acontia of *Metridium senile* and of *Diadumene luciae*, and (b) detachment or other escape responses. In addition, the effect of tentacles, sand on the column, dense groups, and the occurrence of detachment (if present) in *Anthopleura elegantissima* were studied. As a necessary adjunct to a study of defenses, the behavior of *Aeolidia* in detecting and locating prey and in feeding was observed.

MATERIALS AND METHODS

The study was conducted during the summer of 1969 at the Pacific Marine Station, Dillon Beach, California.

Individuals of all species of anemones found in the intertidal zone of various local beaches were collected to be used in the experiments and observations. They were:

Anthopleura artemisia (Pickering, 1848);
Anthopleura elegantissima (Brandt, 1835);
Anthopleura xanthogrammica (Brandt, 1835);
Corynactis californica Carlgren, 1936;
Diadumene luciae (Verrill, 1898) (called *Haliplanella luciae* by Hand, 1955);
Epiactis prolifera Verrill, 1869;
Metridium senile Linnaeus, 1767;
Tealia coriacea (Cuvier, 1798); and
Tealia crassicornis (Müller, 1776).

Anthopleura artemisia lives buried in sand and attached at the base to rocks in protected areas, such as between large boulders, in zones 3 and 4 of Ricketts & Calvin, 1968.

Anthopleura elegantissima occurs on rocks of the protected outer coast or in quiet waters of bays, in zone 3. The anemones occur in large dense masses of individuals which appear to originate from a single individual by longitudinal fission (FORD, 1964; HAND, 1955). Sand, gravel, and bits of shell adhere tightly to the exposed parts of the columns of these anemones.

Anthopleura xanthogrammica, the largest species of the 3, lives in more or less protected areas of the open coast as well as on the protected outer coast in the same localities as *A. elegantissima,* but below that species. The anemones are solitary or occur in small groups which are not as tightly packed as those of *A. elegantissima.*

Corynactis is a very small anemone occurring in protected areas on rocks in the protected outer coast, in zone 3 and below, in dense aggregations. The anemones have capitate tentacles with very large nematocysts.

Diadumene, an introduction from Japan (RICKETTS & CALVIN, 1968), occurs on oyster shells and rocks of bays and estuaries, in zone 2. Acontia are present.

Epiactis occurs in protected areas on rocks and algae in the protected outer coast, and on a variety of solid objects including plants in bays and estuaries, in zones 3 and 4.

Metridium is a large anemone occurring in rocks, wharf pilings, and floats in quiet water, in zone 4 and below. Acontia are present.

Tealia coriacea occurs in rocks in protected areas with shell, sand, and gravel attached to the column and often buried in sand and gravel. This species was difficult to obtain and was not used extensively in the study.

Tealia crassicornis, a large anemone, occurs on rocks of the open coast with *Anthopleura xanthogrammica,* in zone 4 and below.

When size or degree of aggregation of anemones is not mentioned, the anemones are not noteworthy in those respects.

Most of the nudibranchs studied were collected from rocks covered with *Anthopleura elegantissima* on the sandy beach below the marine station. A few were collected from rocks of the north jetty at the entrance to Bodega Bay, on which *A. elegantissima, A. xanthogrammica, Corynactis,* and *Epiactis* were the most abundant anemones. Some nudibranchs were also collected from rocks in Tomales Bay (Nick's Cove) which had *A. elegantissima* living on them. In all, about 20 nudibranchs were collected. Those from each locality were not studied separately, because I was unable to obtain enough individuals from the jetty or Nick's Cove.

EXPERIMENTS PERFORMED

The experiments to determine food preference were of 2 main types:

A. In the first, several nudibranchs were introduced into a plastic cage (30 × 19 × 12 cm) containing (with some exceptions) one individual of each species of anemone

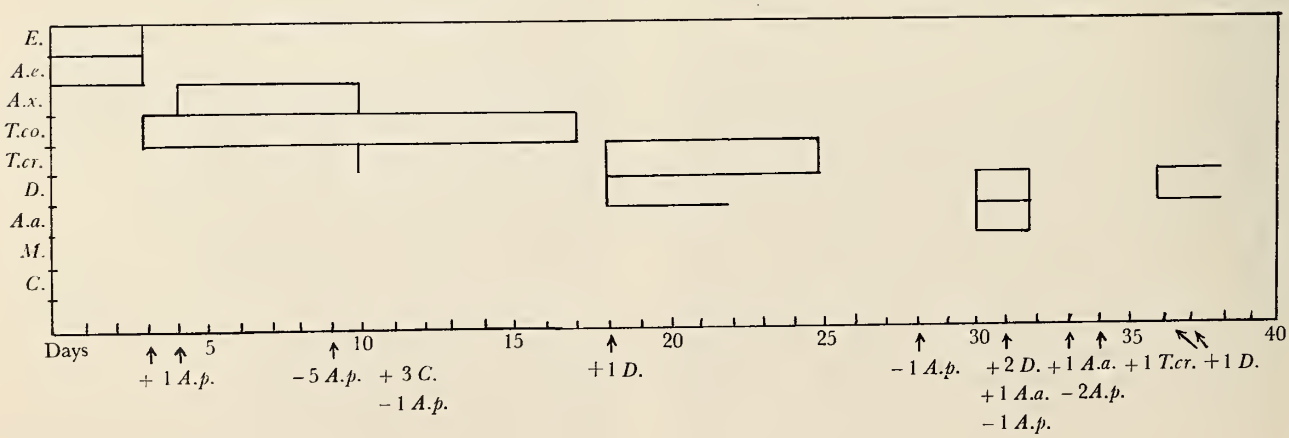

Figure 1

Experiment A, number 1: Number of days *Aeolidia* spent eating the different anemones and order in which they were eaten. Arrows show number of anemones (abbreviated as in Table 3) or nudibranchs (*Ap*) added (+) or removed (—) on that day. Open end of bars indicates anemones were not consumed entirely

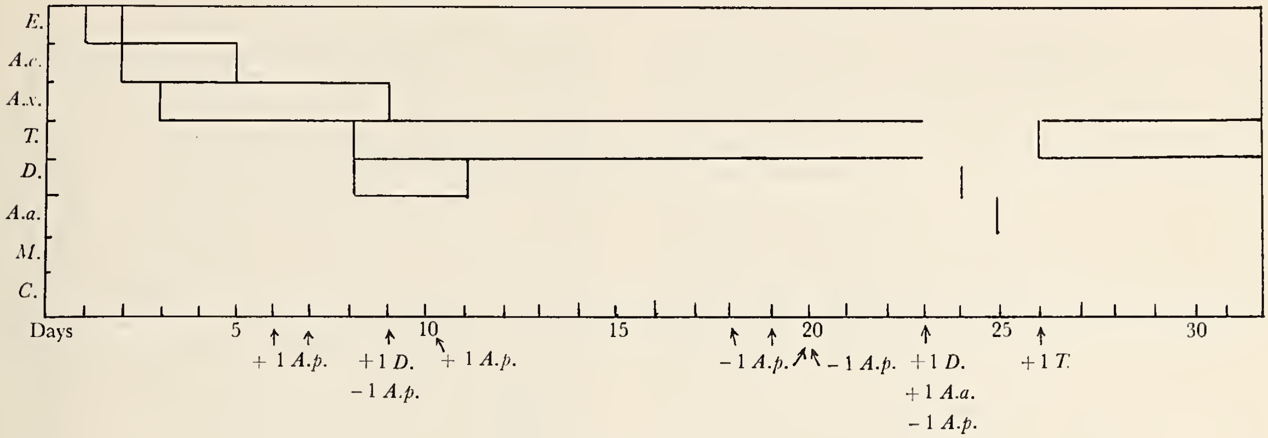

Figure 2

Experiment A, number 2: Number of days spent eating the different anemones and order in which they were eaten. Symbols as in Figure 1; * indicates nudibranch died

which had been allowed to attach. The cages were covered with cheese cloth to prevent escape of the nudibranchs. Two experiments of this type were run simultaneously for most of the research period (6 weeks). Since the cages also served as holding tanks for nudibranchs not being used in other experiments and as sources of nudibranchs for other experiments, the number in the cages shifted from time to time, as did the individuals involved. The duration of each experiment and the changes made in the numbers of nudibranchs present are shown in Figures 1 and 2. The criteria used to determine preference were: (1) which species were eaten; (2) the order in which the anemones were eaten; (3) the length of time taken to consume each anemone, and (4) the proportion of nudibranchs feeding during each observation relative to the proportion doing something else (being inactive or wandering). Observations were generally made twice a day.

B. The second type of food-preference experiment involved offering a group of 2 - 5 nudibranchs a choice between 2 species of anemones which had been put in uncovered glass dishes (11 cm in diameter) and allowed to attach. A few combinations were not used because of lack of time and nudibranchs, and because they were not crucial in determining preference. For the same reasons replications of some combinations were not made. Nevertheless, a given species of anemone was offered to groups of nudibranchs at least 6 times in combination with different species. Judgment of food-preference was based on the same criteria used for experiment A. Again, observations were made twice a day. The experiments were terminated when one or both anemones were completely eaten or when the nudibranchs persistently wandered or escaped rather than eating.

Three further types of experiments were performed to provide information on various aspects of the feeding behavior of *Aeolidia* and defenses of the anemones, and to provide supplementary information on food-preference.

C. To determine whether *Aeolidia* were attracted to food from a distance, a preferred species of anemone was placed upstream from the nudibranchs. In the first 2 experiments, nudibranchs were offered a choice between anemones and water alone to serve as a control for their response to currents. In the third experiment, the responses to 2 species offered at the same time were compared. In all cases water flowed gently into 2 plastic cages (30 × 19 × 12 cm) containing respectively either the anemones and water or the 2 species of anemones. A rubber tube ($\frac{1}{2}$ inch diameter) connected each of these cages with one at a slightly lower level containing the nudibranchs. The upper ones rested on the bottom halves of several plastic petri dishes 8 mm deep. The ends of the tubes extended to the bottom of all 3 cages. Water flowed out of the nudibranch cage through holes bored near the top. The anemones had been put in the bottom half of a petri dish and allowed to attach before being introduced to the cage. The experiments were run for 24 hours, after which the number of nudibranchs in the 3 cages was noted. Only 3 experiments were performed because of insufficient time, space, and nudibranchs.

D. To provide information on the defensive adaptations of anemones and their effect on the nudibranchs, as well as on searching and food-locating behavior of the nudibranchs, nudibranchs were introduced to bowls in which anemones had attached, and the behavior of predator and prey was observed.

E. The last type of experiment dealt with the feeding behavior and activity pattern of nudibranchs offered groups of *Anthopleura elegantissima* and the defenses of this species. Two experiments were performed. In the first, 2 nudibranchs were put into an uncovered enamel pan ($17 \times 29 \times 5$ cm) into which 20 anemones had been placed several weeks earlier and which had attached and spaced themselves out. The anemones were not tightly packed together as in nature but had spaces of several centimeters between most of them, nor did they have sand adhering to their columns. They had been collected from different localities at different times and thus were from different clones. Observations of the behavior of the nudibranchs and anemones were made usually twice a day for 10 days. For the second experiment about 20 anemones were collected from a single area on a rock below the marine station, put in an uncovered round glass dish (14 cm in diameter and 4 cm deep) with adhering sand and loose sand taken from the base of their rock, and allowed to attach. Three nudibranchs were then introduced. This experiment lasted 8 days and observations were made usually twice a day.

RESULTS

EXPERIMENT A, Number 1

At the beginning of the experiment 5 nudibranchs were put with the following anemones:

species	diameter of base (cm)
1 *Anthopleura elegantissima*	2.5
1 *Anthopleura xanthogrammica*	5.0
2 *Epiactis prolifera*	1.0 and 2.5
2 *Metridium senile*	both 3.5
1 *Tealia coriacea*	5.0
1 *Tealia crassicornis*	5.0

Later *Anthopleura artemisia, Corynactis californica, Diadumene luciae,* and another *Tealia crassicornis* were added. The number of individuals of each species added and the timing of the additions are indicated in Figure 1. The size of these anemones was not measured.

Figure 1 shows that the anemones were eaten in a definite order. The first ones eaten were *Epiactis* and *Anthopleura elegantissima.* The smaller *Epiactis* was completely eaten within two hours following introduction of the nudibranchs, while the larger one and *A. elegantissima* were started. The second ones eaten were *Tealia coriacea* and *A. xanthogrammica. Tealia* was attacked within 6 hours and *Anthopleura* within 24 hours after the first anemones were eaten. *Tealia crassicornis* was the last of the original anemones to be eaten. Although this anemone was first attacked on the day *A. xanthogrammica* was completely eaten, very little was eaten then. The nudibranchs did not really begin eating it until the second day after *T. coriacea* had been consumed.

Diadumene (introduced the day before) was attacked the same day as the second attack was made upon *Tealia crassicornis.* This same anemone was never completely eaten, although it was reduced to $\frac{3}{4}$ of the edge of the pedal disk by the 4th day. A period of 5 days elapsed following this day without the nudibranchs having eaten any parts of the remaining anemones: the original *Metridium* and the 3 *Corynactis* added on the 10th day of the experiment. However, the presence of extruded acontia and mucus in the water seen on 3 observations during this time indicated that *Metridium* had been attacked. At the end of this 5-day period, 2 more *Diadumene* and one *A. artemisia* were added. All 3 were soon attacked, and all but the pedal disk of one *Diadumene* were completely eaten within 2 days. The new *A. artemisia* and *T. crassicornis* added soon afterwards were not attacked during the remaining 8 days of the experiment. Likewise, *Corynactis* and *Metridium* were not attacked during this time.

DISCUSSION

Although the nudibranchs showed a distinct preference for certain species, their relative preference for others remained unclear. It appeared that *Epiactis* and *Anthopleura elegantissima* were preferred to others offered, but the preference (if any) between these 2 species was not clear. The fact that the smaller *Epiactis* was eaten before the other 2 (both the same size) indicated that size of prey may play a role in determining food-preference when other things are equal. Although *A. xanthogrammica* and *Tealia coriacea* were the same size and were attacked within a day of each other, *A. xanthogrammica* seemed to be preferred, judging by the comparatively short time taken to consume that anemone and by the smaller proportion of time spent wandering (Figures 1 and 3). The relative preference for *Diadumene* and *A. artemisia* was unclear. The first time the anemones were introduced one *Diadumene* was not completely eaten while *Anthopleura* was, whereas the second time they were added *Diadumene* was partially eaten while the other was not eaten at all. How the preference for *Diadumene* and *Anthopleura* fit into the order of preference for the original anemones could not be determined, since the original anemones were eaten by the time these last 2 were added. Likewise, the relative preference for *Diadumene* and *Tealia crassicornis* was unclear. The fact that both were attacked at the same time indicated equal preference, but the fact that *Diadumene* was not completely eaten indicated a stronger preference for *Tealia*. However, toward the end of the experiment the fact that the new *Tealia* was not eaten at all while 2 of the 3 *Diadumene* were at least partially eaten indicated a preference for *Diadumene*.

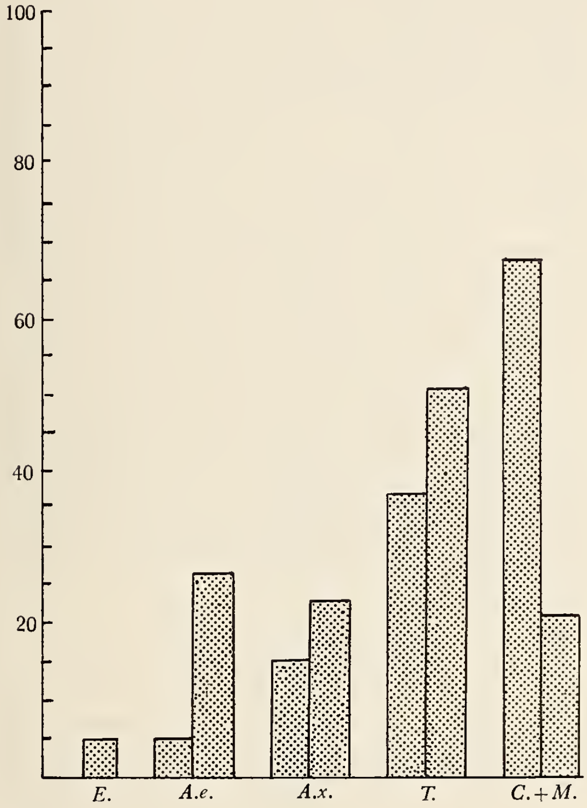

Figure 3

Experiment A, 1 and 2: Percent nudibranchs wandering during the observations made while they were eating each species. Names of anemones abbreviated as in Table 3. The data were obtained by counting the number of nudibranchs wandering during each observation, obtaining the total for the period in which each species was being eaten, and calculating the percent of the total nudibranch-observations. A few anemones were not included because of inconsistent results (*Anthopleura artemisia* and *Diadumene*) or because nudibranchs were not feeding on them during the observations, although they had been eating them previously (*Diadumene,* the smaller *Epiactis* of the first experiment, and the *Epiactis* of the second experiment). The data for *Corynactis* and *Metridium* in the first experiment were obtained only from the period of 5 days in which no other anemones were available. The data for these anemones in the second experiment were obtained during the period beginning after the original *Tealia* had been removed until the end of the experiment, although some anemones were available and were slightly eaten during this time. For both experiments, only the nudibranchs wandering during the time the first *Tealia crassicornis* was being eaten were included in the data for *Tealia*

In summary, the anemones can be arranged in the following order from most to least preferred: *Epiactis* and *Anthopleura elegantissima*; *A. xanthogrammica*; *Tealia coriacea*; *T. crassicornis*; *Corynactis* and *Metridium.* In addition, *Diadumene* and *A. artemisia* were preferred to *Corynactis* and *Metridium.*

EXPERIMENT A, Number 2

At the beginning of the experiment 5 nudibranchs were put with one each of the following species:

species	diameter of base (cm)
Anthopleura elegantissima	3.5
Anthopleura xanthogrammica	3.5
Corynactis californica	0.5
Epiactis prolifera	2.0
Metridium senile	3.5
Tealia crassicornis	7.0

Later *Anthopleura artemisia, Diadumene luciae,* and a new *Tealia crassicornis* were added. The number of individuals involved and the timing of the additions are indicated in Figure 2. The size of the new anemones was not measured.

Figure 2 shows that again the original anemones were eaten in a definite order. *Epiactis,* the first one eaten, was consumed between the 2nd and 3rd day, and *Anthopleura xanthogrammica* was attacked on the 4th day. *Tealia* was attacked on the 9th day, but was never completely eaten. It began to decompose on the 22nd day and was removed 2 days later.

The first *Diadumene* added was attacked on the day of its introduction. Neither the second *Diadumene* nor the

Anthopleura artemisia added later was eaten by the end of the experiment, although 2 days after their introduction a nudibranch was seen feeding on *Diadumene* and one day later one was feeding on *Anthopleura.* The new *Tealia* added still later was never consumed entirely, although it was first attacked on the day after its introduction and was grazed on throughout the rest of the experiment. Neither *Corynactis* nor *Metridium* was eaten, although acontia and mucus were seen in the water during several observations from the 10[th] day to the end of the experiment.

DISCUSSION

The apparent food-preference was similar to that of the first experiment. Again, *Epiactis* and *Anthopleura elegantissima* were the first anemones eaten. That *Epiactis* was eaten first may have been related to its smaller size. The preference for *A. elegantissima* over *A. xanthogrammica* was not as definite as in the first experiment. However, the facts that *A. elegantissima* was attacked first, was eaten in a shorter time (both were the same size), and less time was spent wandering (Figure 3) indicated a preference for that species. *Anthopleura xanthogrammica* was definitely preferred to *Tealia.* Again, the relative preference for *Tealia* and *Diadumene* was unclear. In the first instance it appeared that *Diadumene* was preferred, since it was eaten completely while *Tealia* was only grazed on slightly over a long time; while in the second instance it seemed as though *Tealia* were preferred, since the nudibranchs attacked *Tealia* before they had completely eaten the previously attacked *Diadumene.* There was only slight interest in *A. artemisia* and *Metridium* and none in *Corynactis.*

In summary, the order of preference seemed to be: *Epiactis* and *Anthopleura elegantissima; A. xanthogrammica; Tealia crassicornis; Corynactis* and *Metridium.* In addition, *Diadumene* was preferred to *A. artemisia, Corynactis* and *Metridium.*

These two experiments also revealed something of the predation methods of *Aeolidia.* (1) Generally, one or at most 2 anemones were attacked and fed upon simultaneously. (2) Once begun, the anemones were usually completely eaten (*Diadumene* being the primary exception, of which a portion of the pedal disk was often left). (3) The nudibranchs when not actually feeding on preferred anemones tended to remain inactive, usually near the anemone being eaten. However, when a less preferred species was being eaten or when an anemone was not being eaten at all more of the nudibranchs were wandering when observed (Figure 3). Thus, it seemed that in the latter cases nudibranchs spent more time wandering than when eating preferred anemones.

The great difference between the two experiments in the percent wandering when the data for *Corynactis* and *Metridium* were taken (Figure 3) was probably due to the much greater state of starvation of the second group of nudibranchs, 3 of which had already died of starvation (Figure 2). Evidence that death was due to starvation was the overall decrease in size of the nudibranchs since the beginning of the experiment, as well as a disproportionate decrease in size of the branches of the digestive gland within their cerata. No nudibranchs died during the first experiment. Those of the first experiment had completely eaten 2 large anemones after they had completed *Anthopleura xanthogrammica*: *Tealia coriacea* and *T. crassicornis.* In contrast, those of the second experiment had not even completed the one *T. crassicornis.* Further, the data for the second experiment were taken from a period beginning 2 days later from the onset of the study than for the first group. It is also noteworthy that the nudibranchs of the second experiment consistently spent more time wandering throughout the experiment (except the very end) than did those of the first one, thus spending more energy per unit time.

EXPERIMENT B

The combinations which were offered to *Aeolidia* and the number of times each was offered are indicated in Table 2. The number of experiments in which each species was eaten first, second, or at the same time as the other species, and the species offered with it for each category are shown in Table 3.

The anemones fell into 3 groups which could be ranked from most to least preferred. The first group included *Epiactis, Anthopleura elegantissima,* and *A. xanthogrammica.* These anemones were either eaten first or at the same time as the other species offered. They were eaten simultaneously, however, only with other members of this group (except for 2 experiments in which *Aeolidia* ate *A. elegantissima* and *Diadumene* together). The proportion of nudibranchs wandering when offered anemones of the first group in combination with any other species was less than the proportion wandering when offered only anemones of the other 2 groups (Figures 4 and 5). The 3 species could not be ranked within the group.

The second group included *Diadumene* and *Metridium.* In all cases in which *Diadumene* was eaten first, the anemones offered belonged to the least-preferred group. In 3 experiments it was not eaten at all. *Diadumene* was eaten in a much greater proportion of the experiments involving

Table 2

Combinations of anemones offered to *Aeolidia* in experiment type B. Letters denote each experiment of a particular combination which was performed

Combination	Base Diameter (cm)
Epiactis and *Anthopleura elegantissima*	a. 0.5 and 0.8, respectively b. no data c. both 2.0
Epiactis and *Anthopleura xanthogrammica*	a. 1.5 and 2.5
Epiactis and *Corynactis*	a. 1.5 and 0.8
Epiactis and *Metridium*	a. 1.0 and 1.5
Epiactis and *Tealia crassicornis*	a. 1.5 and 4.0
Anthopleura elegantissima and *A. xanthogrammica*	a. both 3.5
Anthopleura elegantissima and *A. artemisia*	a. both 1.5 b. 2.0 and 3.0
Anthopleura elegantissima and *Corynactis*	a. 1.5 and 0.5
Anthopleura elegantissima and *Diadumene*	a. 1.5 and 0.5 b. 1.5 and 0.5
Anthopleura elegantissima and *Metridium*	a. both 2.0
Anthopleura elegantissima and *Tealia*	a. 4.0 and 3.0
Anthopleura xanthogrammica and *Diadumene*	a. 4.0 and 1.0
Anthopleura xanthogrammica and *Metridium*	a. no data
Anthopleura xanthogrammica and *Tealia*	a. 3.5 and 3.0
Diadumene and *Anthopleura artemisia*	a. 0.5 and 1.5 b. 0.5 and 1.5
Diadumene and *Corynactis*	a. both 0.5 b. both 0.5 c. both 0.5
Diadumene and *Metridium*	a. 1.0, no datum b. both 0.5 c. 0.4 and 0.5 d. 1.5 and 1.0 e. 0.5 and 0.8
Diadumene and *Tealia*	a. 3.0 and 0.5 b. 3.0 and 0.5
Metridium and *Anthopleura artemisia*	a. 0.8 and 1.5
Metridium and *Corynactis*	a. 0.8 and 0.5
Metridium and *Tealia*	a. 0.8 and 3.0
Corynactis and *Anthopleura artemisia*	a. 0.5 and 1.5
Corynactis and *Tealia*	a. 3.0 and 0.5

it than *Metridium* (80% vs. 45%). Nevertheless, it was surprising that *Metridium* was eaten in such a large proportion of the experiments. In 2 instances (when offered with *Diadumene*) it was even the first one eaten. In the other cases, it was eaten only after the preferred one had been consumed. In every case in which *Metridium* was eaten, however, feeding occurred only after I had repeatedly replaced the nudibranchs, which kept escaping to the water table. It is also noteworthy that the anemones were small (1.5 - 2.0 cm). Evidence that the defenses of large *Metridium* may be more effective in preventing predation than those of smaller ones is presented in the section on behavior of *Metridium*. It is further interesting that (except for the cases with *Diadumene*) the nudibranchs ate *Metridium* only after eating other anemones. This fact indicated a greater tendency to attack *Metridium* after the nudibranchs had been feeding for a while than when they had not eaten at all.

The third group included *Anthopleura artemisia, Corynactis,* and *Tealia crassicornis.* These anemones were not

Table 3

Experiment B: Order in which anemones were eaten
Explanation in text

	first		with		together		with		second		with		not eaten		with	
sp.	n	%	sp.	n	n	%	sp.	n	n	%	sp.	n	n	%	sp.	n
E.	4	50	*A.e.*	1	4	50	*A.e.*	3	0	0	–	–	0	0	–	–
			M.	1			*A.x.*	1								
			C.	1												
			T.	1												
A.e.	6	50	*D.*	1	6	50	*E.*	3	0	0	–	–	0	0	–	–
			M.	1			*A.x.*	1								
			A.a.	2			*D.*	2								
			C.	1												
			T.	1												
A.x.	4	67	*D.*	1	2	33	*E.*	1	0	0	–	–	0	0	–	–
			M.	1			A.e.	1								
			T.	2												
D.	7	47	*A.a.*	2	2	13	*A.e.*	1	3	20	*A.x.*	1	3	20	*M.*	3
			C.	3							*M.*	2				
			T.	2												
M.	2	18	*D.*	2	0	0	–	–	3	27	*E.*	1	6	55	*D.*	3
											A.e.	1			*A.a.*	1
											A.x.	1			*C.*	1
															T.	1
A.a.	0	0	–	–	0	0	–	–	0	0	–	–	6	100	*A.e.*	2
															D.	2
															M.	1
															C.	1
C.	0	0	–	–	0	0	–	–	0	0	–	–	8	100	*E.*	1
															A.e.	1
															D.	3
															M.	1
															A.a.	1
															T.	1
T.	0	0	–	–	0	0	–	–	0	0	–	–	8	100	*E.*	1
															A.e.	1
															A.x.	2
															D.	2
															M.	1
															C.	1

E. – *Epiactis*; *A.e.* – *Anthopleura elegantissima*; *A.x.* – *Anthopleura xanthogrammica*; *D.* – *Diadumene*; *M.* – *Metridium*; *A.a.* – *Anthopleura artemisia*; *C.* – *Corynactis*; *T.* – *Tealia crassicornis*; n – number of experiments in each category; % – percent of the total number of experiments with given anemone

eaten at all during the course of the experiments (2 - 6 days). The preferred anemones, in contrast, were usually attacked within a few hours after introduction of the nudibranchs, and were completely eaten by the second or third day, the time taken related to the size of the anemones. When offered the least preferred anemones, the nudibranchs spent a high proportion of time wandering in the bowls or they escaped to the water table where they were frequently eating anemones stored there (Figures 4 and 5.) It is noteworthy that nudibranchs were never seen to be eating the species of the second or third groups on the water table, but only those of the first group.

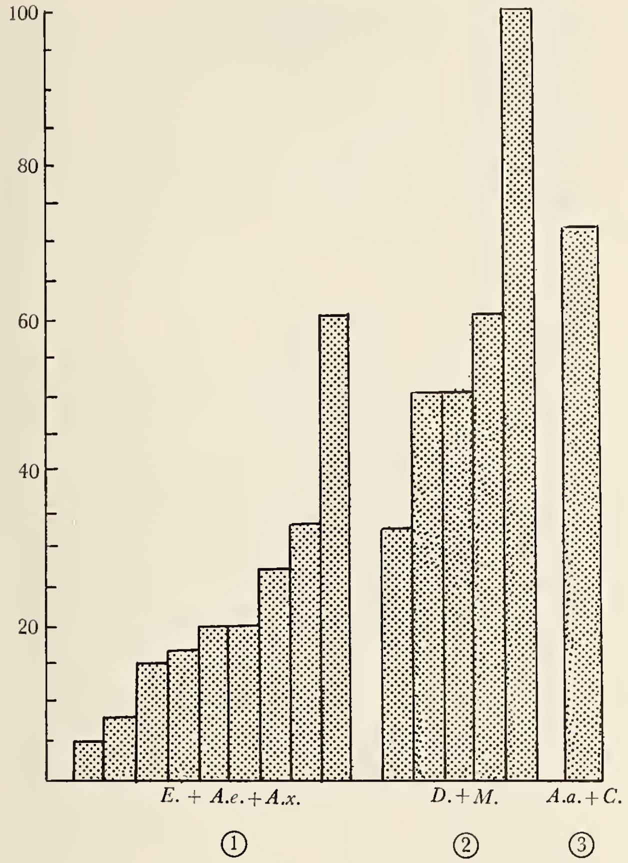

Figure 4

Experiment B: Percent wandering when offered a combination including: (1) the 3 most preferred anemones; (2) the 2 of intermediate preference, and (3) the 3 anemones of least preference. Each bar represents the percent of the total nudibranch-observations involving an anemone in each group in combination with one of the same or of a less preferred group. The observations including an anemone in combination with one of a more preferred group are omitted, since the more preferred species would govern the activity pattern

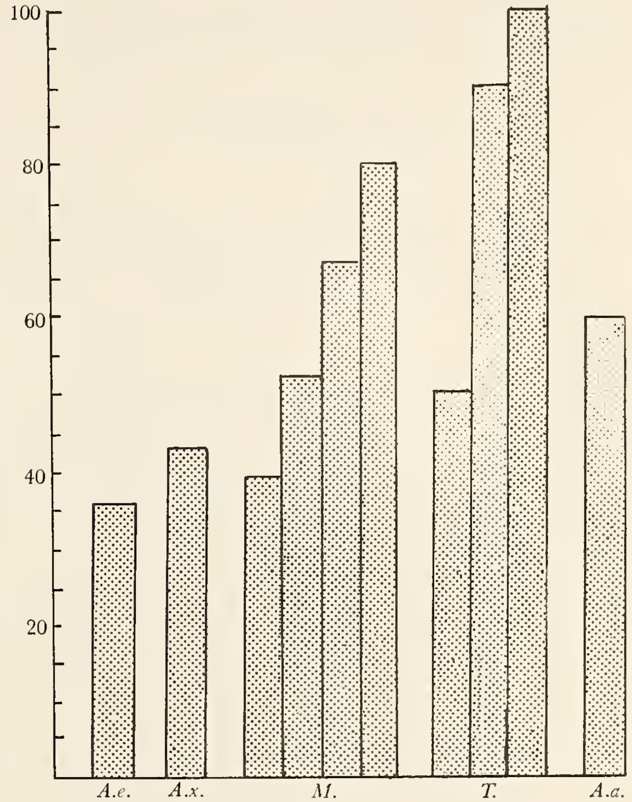

Figure 5

Experiment B: Percent wandering when each anemone was the only one available (after the preferred one had been eaten). Each bar represents the percent of the total nudibranch-observation for the periods in which each anemone was the only one available. Data are unavailable for *Epiactis* (eaten too rapidly), as well as for *Corynactis* and *Diadumene* (not offered alone)

DISCUSSION

The results of this series of experiments showed an order of preference similar to that shown by experiment type A. *Epiactis, Anthopleura elegantissima, A. xanthogrammica* were preferred to all others, and *Corynactis* was not eaten at all. The primary differences included (1) the lack of distinction in type B between the preference for *Epiactis* and *A. elegantissima* on the one hand, and *A. xanthogrammica* on the other; (2) the fact that some *Metridium* were eaten; and (3) the fact that *A. artemisia* and *Tealia* were not eaten at all.

This type of experiment provided further information on predation methods of groups of *Aeolidia.* (1) The nudibranchs fed on the preferred anemones during the same period of time, alternating between the 2 present, rather than eating one totally before attacking the other. (2) They completely consumed all anemones but *Diadumene.* (3) When offered a combination including a preferred species, the nudibranchs spent most of the time either eating or being inactive. They spent a relatively small amount of time wandering: 36% of the nudibranchs observed were eating, 38% were inactive, and only 26%

were wandering. With the less preferred species, however, only 10% were eating, 30% were inactive, and 60% were wandering.

EXPERIMENT C

In the first trial 5 nudibranchs were offered a choice between a group of *Epiactis* and water alone. Within the first 2 hours 2 nudibranchs had arrived in the anemone cage and a third was on its way in the tube. Within 8½ hours all nudibranchs had gone across and were feeding on the anemones.

In the second trial 5 nudibranchs were offered a choice between a group of *Anthopleura elegantissima* and water alone. Two nudibranchs moved across within 9 hours, followed by 2 others within 24 hours from the start of the trial. All 4 nudibranchs were eating when observed. The 5th animal had escaped to the water table.

In the third trial 5 nudibranchs were given the choice between *Epiactis* and *Anthopleura elegantissima*. Within 24 hours one had gone across to each species. The other 3 were in the original cage wandering. Within 24 more hours they had escaped to the water table where they were eating an *A. elegantissima*. Why they did not go across to one of the 2 anemones is unclear. Perhaps they were equally attracted to both species and the resulting strong approach conflict resulted in indecision and ambiguous behavior.

In conclusion, these preliminary experiments showed that *Aeolidia* could use distance chemoreception to detect and locate its prey. That the nudibranchs were attracted to substances released by anemones was further indicated by an observation during a trial run using *Epiactis*. A nudibranch which was put at the end of the control tube (water only) showed no response other than to move away, while the same animal put at the end of the tube from the anemone cage immediately crawled in and arrived in that cage within 15 minutes.

BEHAVIORAL INTERACTIONS OF ANEMONES AND NUDIBRANCHS

1. Searching, Prey Locating, and Feeding Behavior of Nudibranchs

When a nudibranch which had been without food for 2 or more days was put in a bowl with a favored species of anemone (*Epiactis, Anthopleura elegantissima,* or *A. xanthogrammica*), the nudibranch often extended its body and moved the anterior $\frac{1}{3}$ - $\frac{2}{3}$ back and forth in the water with the oral tentacles and rhinophores extended. If the nudibranch did not contact an anemone, it reattached to the substrate and moved forward, perhaps repeating the head-raising behavior several times, and correcting its course to go more directly toward the anemone. Frequently the nudibranch did not raise the anterior part of the body off the substrate, but simply moved forward swinging the head and especially the extended oral tentacles from side to side and frequently touching the oral tentacles to the substrate. The rhinophores meanwhile were also moved around in the water in various directions. During searching the buccal mass was often protruded.

If while searching the nudibranch touched an anemone with the mouth or oral tentacles, it immediately retracted its head, pointed the anterior third of the cerata forward so that the anteriormost ones hid the head beneath them, and contracted the oral tentacles. This general contraction was followed by re-extension of its head and oral tentacles toward the stimulus. When contact occurred again, there was slight retraction, but the nudibranch continued forward, applied its mouth to the anemone, and began to feed. The nudibranchs generally began eating the part of the anemone first contacted (unless it were the tentacles), usually the base of the column. If the tentacles had been contacted (usually causing the nudibranch to retract more strongly than when the column or oral disk were touched), the nudibranchs often began eating the margin of the column just aboral to the tentacles. If while the nudibranch was moving along cerata happened to touch an anemone, the touched cerata contracted sharply, adjacent ones were pointed toward the touched ones, and the whole animal usually contracted. This initial response was followed by extension of the head toward the stimulus, contact (and slight contraction), and feeding.

When nudibranchs were feeding or otherwise inactive, their head, tail, rhinophores, and oral tentacles were retracted so that most of the body was hidden under the cerata. A feeding animal could be distinguished from a non-feeding one by the fact that the buccal mass of a feeding nudibranch was protruded and applied closely to the anemone. In this posture the nudibranchs strongly resembled anemones, especially *Anthopleura elegantissima.*

There was no striking difference in strength of response to contact with any of the anemones except *Corynactis* and *Metridium,* which elicited a stronger contraction. When these 2 anemones were touched the nudibranchs turned and moved away after their initial contraction. The clubbed tips of the tentacles of *Corynactis* adhered tightly to the part of the nudibranch touched, particularly to the cerata, and the nudibranch had to pull hard to free itself. The behavioral interactions of the nudibranch and *Met-*

ridium are described below. The essential difference in response to *Epiactis, Anthopleura elegantissima,* and *A. xanthogrammica* on one hand, and to *Corynactis, Diadumene, Metridium, Tealia,* and *A. artemisia* on the other, was that the nudibranchs usually turned toward and began eating the first 3 species of anemones, but turned and moved away from the latter 5 species. In addition, the nudibranchs usually did not exhibit clear-cut searching behavior when put with the latter anemones.

2. Behavior of Anemones

All anemones contracted sharply upon contact with the nudibranchs, the contraction being more rapid and stronger than when touched gently with a probe. Usually, *Epiactis, Anthopleura elegantissima, A. xanthogrammica,* and *Tealia* bent the column toward the nudibranchs with their tentacles still extended. With repeated or prolonged contact the anemones retracted their tentacles, closed the sphincter muscle around the margin of the oral disk, and contracted the column farther, becoming more or less round. When the nudibranchs began feeding on *Epiactis, A. elegantissima,* and *A. xanthogrammica,* the anemones usually contracted their muscles even more, but without decreasing much in size and losing much water; thus the column became hard and round. The column often tended to be thin-walled or inflated, especially on the side toward the nudibranch.

Epiactis invariably (8 observations) released its hold on the substrate within a few minutes after onset of feeding by a nudibranch. Detachment began in the area closest to the nudibranch and was initiated by contraction of the pedal disk margin, followed by lifting up of the margin and progressive detachment of the entire disk. *Anthopleura elegantissima* also often detached soon after feeding began (7 of 11 observations); *A. xanthogrammica* usually (5 observations) detached, at least partially, within a few minutes of being fed upon. None of the anemones detached when nudibranchs only touched them.

Anthopleura xanthogrammica tended to remain detached for an indefinite period of time after the nudibranchs had ceased feeding and released the anemones, while the other 2 species usually reattached. The reattachment subjectively had a greater tendency to occur in *A. elegantissima* than in *Epiactis.* The released anemones would lie on the substrate rounded up until they reattached.

The *Tealia* and *Metridium* which were eaten in the preference experiments were usually detached but not particularly inflated or turgid when the nudibranchs were eating them. The *Anthopleura artemisia* attacked during the preference experiments were detached and turgid though not particularly inflated while being eaten. *Diadumene* was the only species of anemone which did not detach while being eaten, although it became quite turgid. *Corynactis* never became inflated or detached.

None of the anemones showed a swimming escape response.

3. Behavioral Interactions of the Nudibranchs and *Metridium* and *Diadumene*

Metridium

Metridium showed no response to the presence of a nudibranch unless actual contact was made. Upon instantaneous contact with any part of the nudibranch an anemone immediately retracted its tentacles and contracted the column, although it usually did not extrude acontia. When small (less than 2 cm diameter) anemones were observed under a dissecting microscope, the acontia on the side touched could be seen to move upward and outward toward the nudibranch. Acontia were usually not extruded unless prolonged or repeated contact was made. When further contact was not made the anemone would soon re-extend itself and appear normal. When further contact was made, however, the anemone contracted again even more strongly, extruded acontia in the region of contact, and closed its sphincter over its tentacles and oral surface, remaining in that state for an indefinite period of time. Gentle contact of an expanded anemone with a probe caused only slight contraction, soon followed by re-extension.

The length of time of prolonged contact by a nudibranch necessary to cause extrusion varied somewhat. In a series of 8 observations, extrusion occurred after $\frac{1}{2}$ to 6 minutes with an average of 2.6, most occurring in 2 to 4 minutes. When the anemones were gently touched with a probe, in contrast, extrusion did not occur until after at least 8 minutes of repeated touching.

It is noteworthy that extrusion often continued after the nudibranch had left, and that the extruded acontia which remained attached to the anemone were eventually retracted.

When a nudibranch touched an acontium, it strongly contracted its whole body, especially the part touched, and turned sharply, moving away from the stimulus. All parts of the body were sensitive, including the foot. The nudibranch also secreted large amounts of viscous mucus. Usually the acontia became entangled in the mucus along with large numbers of discharged nematocysts. Whenever an acontium happened to contact the nudibranch itself, usually a ceras, it adhered tightly. When this happened, the nudibranch quickly and strongly contracted and bent the ceras to which the acontium was attached (sometimes autotomizing the ceras), erected the others and generally pointed them toward the stimulus, and tried to move away.

Although the nudibranchs used in the behavioral observations managed to free themselves, on 3 successive days in experiment A - 1 nudibranchs were found wrapped in thick mucus with acontia caught in the mucus and wrapped around some cerata. The first nudibranch was removed and placed on the water table where the next day it appeared normal except for contracted cerata in one area, and was feeding. It appeared to be completely recovered within 3 days. The other 2 nudibranchs were left in the cage where they recovered within one day.

Toward the end of experiment A - 2 a nudibranch was found nearly dead with the body wall of its back broken and with some of the viscera protruding through the hole. It is probable that it had been injured by acontia, although none were extruded at the time of observation, because the nudibranchs had been attacking *Metridium* during the past few days. Although it is possible that another nudibranch had attacked it, that possibility is unlikely because I saw no other evidence of possible cannibalism even after some nudibranchs had been without food for 3 weeks. Rather, it seems as though these 3 nudibranchs were weakened enough from starvation that their defenses were no longer effective.

Boutan (1898) noticed the same weakness in an *Aeolidia* spent from spawning which was not able to escape from an anemone onto which he had dropped it, but was taken in and digested. Healthy ones he had dropped onto an anemone were able to escape. I also found that anemones (*Anthopleura elegantissima* and *A. xanthogrammica*) would accept and digest dead or weakened nudibranchs. The feeding response was not just due to lack of a defensive response of the nudibranchs, but due to their own lack of defensive response as well.

That acontia were a very strong deterrent to predation was observed on many occasions. (1) Sometimes nudibranchs after their initial withdrawal upon contact with *Metridium* re-approached it with the buccal mass protruded and explored it with their oral tentacles and oral surface. This invariably elicited extrusion of acontia, and upon contact with them the nudibranchs contracted sharply and moved away. (2) On many occasions in choice experiments involving *Metridium*, threads of mucus were seen crisscrossing the bowl, with acontia, discharged nematocysts, and sometimes autotomized cerata caught in them, while *Metridium* remained intact.

Similarly, Yarnall (personal communication) frequently noticed in the field that *Aeolidia* in Monterey Bay, California, would cease feeding when acontia became entangled in their cerata. The nudibranchs in the laboratory which became entangled and could not free themselves died within 24 hours. He also found several moribund nudibranchs with acontia entangled in their cerata in the field. Nevertheless, he commonly found acontia in the stomachs of *Aeolidia*. Harris (1971) found that the defenses of *Metridium* usually prevented the nudibranchs from feeding on large anemones in New England. Some preliminary experiments I did showed that perhaps the local nudibranchs would also eat small ones but not larger ones. The effectiveness of the defenses of *Metridium* of different sizes merits further investigation.

Diadumene

The mutual responses of the nudibranchs and *Diadumene* were much less definite than those of the nudibranchs and *Metridium*. Again, contact was necessary to elicit a response. Upon contact, an anemone retracted its tentacles, partially contracted its column, and moved acontia upward in the region of the stimulus. Upon repeated or prolonged contact, the tentacles were retracted completely, the sphincter around the margin of the oral disk was contracted, hiding the tentacles, and the column was contracted strongly against the water inside. The acontia were moved farther upward or outward and were often extruded. Acontia were extruded once when a nudibranch crawled over an anemone, and once when one bit and began feeding on an anemone. The latter nudibranch continued eating, ignoring the acontia. Acontia generally caused the nudibranchs to withdraw slightly, but the nudibranchs did not respond significantly more strongly to acontia than to any other part of *Diadumene*. Their response to contact with any part of an anemone was like that to contact with a probe. Likewise, the anemone's response was not significantly different from that to such contact.

FEEDING BEHAVIOR AND ACTIVITY PATTERN OF NUDIBRANCHS OFFERED GROUPS OF *Anthopleura elegantissima*, AND DEFENSIVE RESPONSES OF THE ANEMONES

There were numerous difficulties in determining activity patterns. Individual nudibranchs and anemones were often difficult to recognize, and this was complicated by the fact that new nudibranchs would appear in the dishes and the ones being studied would disappear. The latter difficulty especially occurred during the second experiment, which took place in a submerged dish which was downstream from other anemones, including a partially eaten *Anthopleura xanthogrammica* to which the nudibranchs kept migrating. However, certain aspects of the activity pattern of the nudibranchs and of the behavior of the anemones became apparent.

1. The nudibranchs did not keep their hold on an anemone once they had attacked it initially, nor did they usually remain inactive nearby. Rather, they let go and wandered off when not feeding.
2. Periods of eating (lasting a few minutes to a few hours) alternated with periods of inactivity of longer duration (several hours to several days), and sometimes with periods of wandering as well.
3. In the absence of a definite current of water flowing over them (first experiment), the nudibranchs tended to eat individuals within a group only partially, rather than tending to consume one before moving to another. For example, at the end of the first experiment, after a nudibranch had been feeding within a group of 10 anemones for 4 days, there were pieces of 5 anemones (rims of pedal disks) and 4 slightly damaged anemones (epidermis missing in places) remaining. Only one anemone had disappeared. However, when a unidirectional current flowed over the nudibranchs (second experiment), it seemed as though they tended to attack and consume one anemone before attacking another. For example, the nudibranchs kept moving upstream to feed on the *Anthopleura xanthogrammica* mentioned above, rather than remaining with and feeding on the anemones in the group. Nevertheless, when not moving upstream the nudibranchs moved from anemone to anemone within the group without consuming any of them.
4. The anemones attacked during the second experiment (in which most of the anemones were in contact with each other) were those on the edge of small groups or which were solitary. The nudibranchs usually did not crawl over anemones to eat one in the midst of a group.
5. Relatively few anemones detached. Of 45 observed anemones 10 (22%) detached. About half of these reattached when left alone. The others remained detached, lying rounded up on the bottom, even though they had little damage and were not attacked again.
6. The attached anemones tended to move away from the nudibranch as they were being eaten and to continue moving after the nudibranch had stopped eating, so that within 24 hours an anemone had often moved 5 cm or more away from its location when first attacked (one anemone moved 5 cm in 4 hours). Some continued moving for several days (20 cm in 3 days, in one case).
7. The anemones in the second experiment dropped most of the sand adhering to them when collected when they were left undisturbed to attach before the nudibranchs were introduced, and they kept dropping the sand I repeatedly poured over them, making it impossible to determine the effect of sand on predation.

GENERAL DISCUSSION AND CONCLUSIONS

Food Preference

On the basis of experiments A and B, the anemones can be put into 3 groups which can be ranked from most to least preferred.

Group I includes *Epiactis prolifera, Anthopleura elegantissima* and *A. xanthogrammica.* These anemones were eaten whenever they were offered, were eaten first when nudibranchs were offered a choice between them and anemones of the other 2 groups, and were consumed rapidly with little wandering. The relative preference for the anemones within this group was less definite. Experiment A, however, provided some evidence that *Epiactis* and *A. elegantissima* may be preferred to *A. xanthogrammica* (see discussions following experiments). Field observations indicated a preference for *A. elegantissima.* Most of the nudibranchs were found on rocks with that species rather than with *Epiactis* or *A. xanthogrammica.*

Defenses seemed to play no role in determining which of the 3 anemones was preferred. Defenses involved nematocysts, inflation, detachment, and (indirectly) size (which appeared to be related to toughness). Only size seemed to govern the order and rapidity with which the anemones were eaten. *Aeolidia* ate the anemones in spite of the difficulties caused by nematocysts, or possible difficulties in maintaining a hold or in biting and rasping the anemones caused by inflation. Detachment caused no problem as long as the nudibranchs were eating, for they held the prey tightly. However, inflation coupled with detachment could be of value when the nudibranchs let go after feeding, by enabling the anemones to roll away. Detachment alone could be of value to large anemones, such as *Anthopleura xanthogrammica,* which could be torn from a nudibranch's grasp by a sudden surge of water or by its own weight. An additional defensive response of *A. elegantissima* was to move away as a nudibranch was eating it and to continue moving after the nudibranch had ceased feeding. This behavior would be safer than detaching, which is likely to result in an anemone falling onto an unsuitable substrate or being washed ashore.

Group II includes *Diadumene luciae* and *Tealia crassicornis,* both of which were sometimes eaten at least in part. They were not the first ones eaten, were often eaten only partially, and were eaten over a longer period of time, and more time was spent wandering than when anemones of group I were being eaten. In addition, nudibranchs were never seen near these species in the field.

Defenses did not seem to be important deterrents in the laboratory. Defenses included the nematocysts of both, the acontia and inflation of *Diadumene,* and the detachment and large size of *Tealia.* However, the bending in *Tealia* and those of group I of the column with still extended tentacles toward the nudibranch could be of advantage by causing the nudibranch to recoil. In recoiling it could contact another anemone which may be in a better position for attack. During several observations nudibranchs did not attack the first anemone they touched, but resumed searching after recoiling eventually to attack another anemone which they encountered.

Tealia was about the same size as the *Anthopleura xanthogrammica* used in the study, had equally effective defenses, and was made equally available in the laboratory, yet the nudibranchs distinctly preferred *Anthopleura.* Examination of the feces of nudibranchs which had been eating each species alone for several days indicated greater physiological adaptation to eating *Anthopleura* than *Tealia.* The feces of nudibranchs which had been eating the red anemone *Tealia* were pink. When examined microscopically, the feces proved to be full of discharged nematocysts, pink cells including some living clumps with beating flagella, and many ciliate protozoans. Those which had been eating *A. xanthogrammica* had white feces containing undischarged nematocysts, ciliates (the observed differences in the ciliate fauna were not investigated), and zooxanthellae. No intact living cells from the anemone itself were present. Amorphous white granular material probably represented undigested remains of the anemone. Although the nudibranchs seemed to be less efficient in processing *Tealia, Tealia* was able to support them well enough for them to lay eggs (which were pink instead of white as when eating *Anthopleura*), grow, and store food in the digestive gland (which was pink instead of green as when eating *Anthopleura*). The relative weights of the 2 anemones which must be eaten to provide the same rate of growth and egg production would be interesting to investigate.

The observations of *Tealia* suggest that learning may play a role in food preference. The only time a *T. crassicornis* was eaten completely, rapidly, and with little wandering was in experiment A - 1. This anemone was the original one in the cage and was attacked soon after *T. coriacea* had been consumed. The second *T. crassicornis,* added well after the first had been eaten, was not eaten at all. The *T. coriacea* was declining when attacked early in the experiment. The tendency of *Aeolidia* to attack wounded anemones is reported in the literature (e. g. Stehouwer, 1952). Thus, it is possible that the nudibranchs had a greater tendency to attack *T. coriacea* than they would have had if the anemone had been healthy. The fact that the original *T. crassicornis* was attacked soon after *T. coriacea* had been eaten while neither the new one nor those in other experiments were attacked, indicates that the nudibranchs may have become conditioned to eating this genus. The fact that the new *Tealia* added later was not attacked indicates that the conditioning must be frequently reinforced to persist. The possibility of conditioning is discussed further below.

Group III includes *Anthopleura artemisia, Corynactis californica,* and *Metridium senile.* These anemones were eaten very rarely, if at all. Further, the nudibranchs were not found with them in the field, although at least *Corynactis* and *Metridium* were very common and occurred in dense groups. *Anthopleura* and *Metridium* were preferred to *Corynactis,* the only anemone which was never eaten at all. The defenses of *Anthopleura* investigated were similar to those of the anemones of groups I and II, yet the anemones were very rarely eaten.

In contrast to all other species, the defenses of *Corynactis* and *Metridium* were an effective deterrent to predation. That is not to imply that without their defenses the nudibranchs would eat them readily. In fact, *Aeolidia* would not attack *Corynactis* even when the tentacles were retracted within the closed oral disk area. Nevertheless, the nudibranchs exhibited a very strong negative response to the clubbed tips of the tentacles of *Corynactis* and to the acontia of *Metridium.* Both of these were potentially dangerous, as behavioral observations showed. The primary defenses of nudibranchs against acontia were their abilities to secrete copious amounts of viscous mucus which prevented discharged nematocysts from touching their epidermis, and to pull away from acontia which managed to adhere despite the mucus. Weakened animals became entangled in acontia; escape was accompanied by loss of entangled cerata. Healthy animals also tended to lose cerata to which acontia had attached. Their defense against *Corynactis* was simply to contract strongly and pull away. It was interesting that the acontia of *Diadumene* did not elicit a strong avoidance response or the secretion of mucus.

Tealia, Diadumene, and *Metridium* are also mentioned in the literature as being eaten by *Aeolidia* (Table 1). Likewise, none of the workers indicated that *Tealia* was the preferred species. However, Swennen (1961) cited unpublished observations of *Diadumene* being preferred to *Metridium. Metridium* was indicated by two workers to be a preferred species and by 4 others as being eaten, including Swennen who raised young nudibranchs on it.

In addition to these published observations on *Metridium,* 4 people (L. Harris, V. Human, T. Gosliner, and J. Yarnall) have told me that they have found large numbers of *Aeolidia* among the abundant *Metridium* on submerged pilings (particularly in Monterey Bay, California), and have either seen the nudibranchs feeding on *Metridium* or have seen evidence that they feed on this species. Harris (personal communication) found the same relationship on the Atlantic coast of the United States as well as in Monterey. Only Harris and Yarnall noticed any particular adverse effect of acontia on the nudibranchs. However, they (like RUSSELL, 1964) noted that the nudibranchs would eat the acontia. The fact that few if any other anemones were present in the habitats observed suggests that perhaps in the absence of less dangerous prey the nudibranchs may learn to cope with the defenses of *Metridium* and come to eat the anemones in spite of the defenses. WOOD (1968) found that the prosobranch *Urosalpinx cinerea* (Say, 1822) had an increased tendency to feed on a species after eating it for a while, which he called "ingestive conditioning." Similar ingestive conditioning may occur in *Aeolidia* as suggested by the present observations on *Tealia* and those just described on *Metridium.* This possibility is supported by the observations of Yarnall (personal communication) that the nudibranchs which had been eating *Metridium* preferred *Metridium* even when given a choice between it and *Epiactis,* while those which had been eating *Epiactis* preferred that species to *Metridium.* However, Gosliner and Harris (personal communication) observed that the nudibranchs which had been eating *Metridium* preferred *Anthopleura elegantissima* when given a choice between it and *Metridium.* Ingestive conditioning was unlikely to have been governing the relative preference of the nudibranchs I studied for the 3 most preferred species, because they did not prefer *A. elegantissima* to *Epiactis* or *A. xanthogrammica,* although most had been feeding on that species before being collected. However, the lack of conditioning could explain why they would not eat *Metridium.* The various ramifications of ingestive conditioning would be interesting to investigate.

In conclusion, the facts that (1) when anemones were made equally available in the laboratory the nudibranchs exhibited definite preferences, (2) the defenses of the anemones other than *Corynactis* and *Metridium* were equally effective, and (3) ingestive conditioning was unlikely to be important in the nudibranchs studied, indicate that preference for particular anemones was not proximately determined by these 3 possible factors alone.

A fourth possible proximate factor is the relative nutritional value of the different anemones. Nutritional value would be related to the rapidity with which the anemones are eaten and digested and to the efficiency of processing by the nudibranchs, as well as to the original nutrient content. The efficiency with which nudibranchs can handle their prey and extract the nutrients would presumably be genetically based and be the result of evolutionary adaptations to eat and digest particular species. Thus relative nutritional value would involve an interaction between the nutrient makeup of the anemones and the processing efficiency of the nudibranchs. The potential nutrient value of the prey, however, would presumably be important as an ultimate factor in the evolution of food-preference and the concomitant feeding adaptations. These two aspects of nutritional value were not investigated as such, but the observations of the feces of nudibranchs which had been feeding on *Anthopleura xanthogrammica* or *Tealia* indicate that the nudibranchs may have different abilities to process the various species.

Relative palatability is a fifth possible proximate factor. Similar to nutritional value, this factor would be expected to involve an interaction between the original defensive adaptations (including the possession of distasteful or painful characteristics) of the prey and evolution of preference in the predator along with the co-occurring adaptations involved with handling the prey's defenses. Thus, palatability is more likely to be dependent on the evolution of food-preference than on some intrinsic property of the prey. To the extent that the relative degree to which a particular species was eaten is a measure of relative palatability, this possible factor was investigated.

Since some of the main possible proximate factors behind food-preference were either unimportant or depended in part on the adaptations of the predator, it seems that preference may be genetically determined in the local populations of *Aeolidia.* The evolution of preference may have been ultimately based on these factors, but they do not seem important any longer. Evidence is presented later that the evolution of preference for at least *Anthopleura elegantissima* and *A. xanthogrammica* may be related primarily to the tendency for these two species to occur in dense concentrations.

The hypothesis that preference is genetically determined is supported by the prediction (among others) made by EMLEN (1966) on the basis of a mathematical model that other things being equal, animals would be more selective when satiated and more indiscriminate when starved. His model concerned the caloric value and consumption times of different foods as a prediction of which ones would be eaten. Since *Aeolidia* was selective even when starving, it would seem as though something were operating to govern food-preference (other than degree of starvation relative to caloric value and consumption times of different foods), which is probably genetical predisposition for the reasons just presented.

Searching and Feeding Behavior

Experiment C, behavior observations, and the fact that escaped nudibranchs tended to congregate around and feed on the same anemone indicate that *Aeolidia* is attracted to its prey from a distance. In addition, contact of anemones especially with the oral tentacles was an important method of location and identification of prey. During searching the oral tentacles were greatly extended and swung from side to side as if feeling for something, and the behavior upon contact depended upon whether or not the touched anemone was a member of a preferred species.

Feeding on preferred anemones continued without interruption for a few minutes to several hours and usually ceased before the anemone was completely consumed. The principal exceptions involved small *Epiactis* and *Anthopleura elegantissima* which the nudibranchs ate rapidly with no observed cessation of feeding. Feeding rate seemed to depend on size of anemone (with size and state of starvation of nudibranchs equal), but when size of anemone was constant, the rate seemed to depend on the degree of toughness of the anemones. Although absolute feeding rate was not investigated, the subjective impression was that *Epiactis* was eaten the most rapidly for its size, followed by *A. elegantissima* and *A. xanthogrammica* in that order. Based on the translucence of the column and the thickness of the body wall, it seemed that *Epiactis* was the most delicate anemone, followed by *A. elegantissima* and *A. xanthogrammica.* The other anemones were not eaten regularly enough for an estimate to be made of the rapidity with which they were eaten.

Nudibranchs began feeding on any part of the anemones except the tentacles, although they rarely began with the oral disk. The principal damage to anemones which had been abandoned after the initial attack was to the epidermis and outermost layers of the underlying tissues. After a longer time and after several feeding periods the nudibranchs would often have eaten through the wall of the column to the gastrovascular cavity. Often the anemones were not abandoned until they had been reduced to doughnut-shaped pieces, apparently the rims of the pedal and oral disks. It is noteworthy that (judged subjectively) these parts were thicker and tougher than other parts of the column. When other preferred anemones were not available, the nudibranchs ate the entire anemone, including these rims, the tentacles, septal filaments, and even the acontia of *Metridium* and *Diadumene.*

When an abundance of a preferred species (*Anthopleura elegantissima* in experiment E) was available, the nudibranchs tended to begin a new anemone once they had ceased feeding and had let go of the first one. This tendency was caused partially by the behavior of the anemone: detachment and falling to the bottom or moving away on the pedal disk. It was also caused by the behavior of the nudibranchs, which let go after feeding. They sometimes began wandering upon cessation of feeding, but more frequently the nudibranchs remained quiescent for several hours and began wandering later. The later wandering seemed to be governed by hunger, and the anemone attacked seemed to be the first one contacted in its wandering in the absence of a definite current of water flowing over the animals. The first anemone contacted usually was not the original anemone, which had escaped from the immediate area.

In a definite current of water the nudibranchs seemed to be attracted to wounded anemones as STEHOUWER (1952) found, since they congregated around single anemones upstream even when intact anemones were closer. In experiment E - 2 the scent of the wounded *Anthopleura xanthogrammica* exerted a stronger attraction than even the wounded *A. elegantissima* nearby on which the nudibranchs had been feeding. Yarnall (personal communication) saw good evidence that *Aeolidia* is attracted to damaged anemones (*Metridium*) in the field. In areas of dense concentrations of *Metridium* he found that the nudibranchs would be clustered around and feeding on a single anemone rather than being evenly scattered throughout the group of anemones and feeding alone. In the absence of a definite current, however, I found that the nudibranchs usually ate alone. The nudibranchs presumably ate alone because (1) they did not detect the anemones which nearby nudibranchs were eating, (2) the strength of the scent from anemones being eaten by nearby nudibranchs was not strong enough to attract them over the scent of or contact with nearer intact anemones, so that they consequently attacked the first anemone they found, or (3) the scent from nearby wounded anemones coming from different directions confused the nudibranchs, causing many changes in direction while wandering which might or might not result in the location of a wounded anemone. These possibilities may also explain why during experiments with a definite unidirectional current the nudibranchs tended to eat the anemones completely before attacking another, while they tended to wander from anemone to anemone in experiments without a definite current.

The facts that nudibranchs tended not to feed constantly until an anemone was completely consumed, that they let go when not feeding, that *Anthopleura elegantissima* escaped by either detaching or moving away on its pedal disk, that nudibranchs followed an inactive period by wandering and tended to attack the first anemone contacted (at least in still or turbulent water), and that nudibranchs tended to attack isolated anemones or those on the edge of groups, could have provided selective pressure in the evolution of grouping behavior in *A. elegantissima*. Grouping would minimize the chances that a given individual would be consumed.

Grouping would also benefit the nudibranchs, as it would provide an abundant source of food concentrated in definite localities enabling the nudibranchs to spend a minimal amount of time and energy searching for food. Further, *Anthopleura elegantissima* is not subject to large fluctuations in population size with the seasons. It is possible that *Aeolidia* is evolving specificity for *A. elegantissima*, since most nudibranchs in nature were with this species. Whether the local distribution of *Aeolidia* is governed by settlement preferences of the veligers or by searching of the postlarval stages would be interesting to discover.

Abundance, dense concentrations of individuals, and population stability are characteristics which would be necessary in a prey population for food specificity of a predator to evolve (MacArthur, 1961; Pianka & Pianka, 1970). One would expect specificity to evolve whenever possible, as it would enable the evolution of specific adaptations to handle the food efficiently. Further, it would be better for behavior to be controlled so that the nudibranchs would remain in an area of suitable food, rather than wandering here and there as they detect different species, as it would minimize the time and energy spent in the search for food.

Anthopleura elegantissima would be superior in at least some of the above attributes to the other anemones studied, with the possible exception of *A. xanthogrammica*. The latter species also occurs in great abundance and is a much larger anemone. Thus, one individual would provide food for a longer time, and the total biomass per unit area may be greater than for *A. elegantissima*. Possible disadvantages of specializing on *A. xanthogrammica* would include the more scattered distribution of individuals, the greater difficulty (with less digestive efficiency?) of eating a larger anemone with presumably tougher and thicker layers of connective tissue, and the greater potential effectiveness of detachment of a larger and heavier anemone.

SUMMARY

Food-preference, the effect of the defenses of the prey on predation, and feeding and prey-locating behavior of the anemone-eating nudibranch *Aeolidia papillosa* on the central California coast were investigated.

Based on the experiments and observations, the following generalizations can be made:

1. The 8 principal species of anemones occurring intertidally can be put into 3 groups depending on the degree of preference shown for them, with the order within the groups remaining unclear. From most to least preferred, the groups are:
   I *Anthopleura elegantissima, A. xanthogrammica, Epiactis prolifera*;
   II *Diadumene luciae, Tealia crassicornis*;
   III *Anthopleura artemisia, Corynactis californica, Metridium senile.*

   The lack of preference for *Metridium* here differs from the distinct preference reported in the literature for European *M. senile*. The lack of preference seemed to be primarily due to the strong aversion of the nudibranchs to acontia. The extrusion of acontia was a definite defense response which invariably occurred when *Aeolidia* repeatedly and prolongedly contacted *Metridium*. The nudibranchs responded by secreting copious and viscous mucus, withdrawing sharply, and moving away.

2. Food preference seemed to be genetically determined, rather than being proximately due to:
   a) defenses of the prey (except for the acontia of *Metridium* and nematocysts of the tentacles of *Corynactis*). The defenses observed were: nematocysts (present in all anemones); inflation of the column (present in *A. elegantissima, A. xanthogrammica, Epiactis, Diadumene, Metridium*); detachment from the substrate (*A. artemisia, A. elegantissima, A. xanthogrammica, Epiactis, Tealia, Metridium*); and acontia (*Diadumene, Metridium*);
   b) accessibility of prey in nature;
   c) learning (although evidence is presented which suggests that this may modify genetically determined preference);
   d) relative nutritional value of different species of anemones;
   e) relative palatability of the different species.

3. *Aeolidia* could detect and was attracted to the anemones of group I at a distance, and exhibited characteristic searching behavior. Prey location and identification were aided by contact of the anemone with the oral tentacles. Location by contact seemed to be the primary prey-detection mechanism in the absence of a definite current of water flowing over an anemone to the predator. In a definite current distance chemoreception seemed to be more important, and wounded

anemones exerted a stronger attraction than intact ones.

4. In regard to feeding activity pattern:
   a) Nudibranchs did not tend to feed continuously until an anemone was consumed;
   b) they released the anemone when not feeding;
   c) they tended to attack the first anemone of the preferred species contacted in the absence of a definite current of water;
   d) feeding was followed by an inactive period which in turn was followed by a period in which the nudibranchs wandered;
   e) only in the absence of other individuals of a preferred species did the nudibranchs consume an anemone completely.

5. The characteristics of the feeding behavior just described plus the fact that *A. elegantissima* either detached when being fed upon and fell to the bottom when released, or moved away on its pedal disk after being released, could make the occurrence of this species in dense masses of individuals an adaptation which would minimize the chance that a particular individual would be eaten.

6. Nearly all nudibranchs used in the study were found with *A. elegantissima*, rather than with the other species of anemones. This species would be predicted on theoretical grounds to be ideal prey for a food specialist (other things being equal). It is possible that specificity for *A. elegantissima* may be evolving in the local populations of *Aeolidia papillosa*.

ACKNOWLEDGMENTS

This study was conducted at Pacific Marine Station, Dillon Beach, California. I wish to express my sincere gratitude to Mr. David H. Montgomery, a visiting instructor, and to Dr. Edmund H. Smith, Director of Pacific Marine Station, for making my stay possible, and especially to Dr. Smith for his generous allocation of work space. I also wish to express my deep appreciation to Mr. Montgomery for all his enthusiasm and interest during the project, for his invaluable help in collecting the animals, and particularly for his careful reading of the manuscript. I wish to thank my husband, Dr. James F. Waters, for all his encouragement, advice, and patience during the preparation of the manuscript. Larry Harris, Vernon Human, Terrence Gosliner, and Jack Yarnall are in my debt for telling me of their observations of *Aeolidia* and *Metridium*, and making me realize that learning in *Aeolidia* may be more important than I had thought. My thanks also go to Jack Yarnall for his helpful comments on the manuscript. The students of the invertebrate zoology class, especially Miss Linda Welch, assisted me greatly in collecting the nudibranchs.

Literature Cited

Boutan, Louis
1898. Moeurs de l'*Eolis papillosa* Linné. Arch. Zool. exp. gén. ser. 3, no. 6, notes & rev. no. 10: XXXVII - XLII

Braams, W. G. & Hannie F. M. Geelen
1953. The preference of some nudibranchs for certain coelenterates. Arch. néerl. Zool. 10 (3): 241 - 264

Eliot, Charles N. E.
1910. A monograph of the British nudibranchiate Mollusca. Suppl. Ray Soc. London, part IV: 198 pp.

Emlen, J. M.
1966. The role of time and energy in food preference. Am. Nat. 100 (916): 611 - 617

Ford, C. E.
1964. Reproduction in the aggregating sea anemone, *Anthopleura elegantissima*. Pacif. Sci. 18 (2): 138 - 145

Hand, Cadet
1955. The sea anemones of central California, Part II: The endomyarian and mesomyarian anemones. Wasmann Journ. Biol. 13 (1): 37 - 99
1955. The sea anemones of central California, Part III: The acontiarian anemones. Wasmann Journ. Biol. 13 (2): 189 - 251

Harris, Larry
1971. Ecological observations on a New England nudibranch-anemone association. The Echo 4: 22

MacArthur, Robert H.
1961. Population effects of natural selection. Amer. Nat. 95 (882): 195 - 199

McMillan, N. F.
1942. Food of nudibranchs. Journ. Conch. London 21: 327

Miller, Michael Charles
1961. Distribution and food of the nudibranchiate mollusca of the South of the Isle of Man. Journ. Anim. Ecol. 30: 95 - 116

Pianka, E. R. & H. D. Pianka
1970. The ecology of *Moloch horridus* (Lacertilia: Agamidae) in Western Australia. Copeia 1970 (1): 90 - 103

Ricketts, Edward F. & Jack Calvin
1968. Between Pacific tides. Stanford Univ. Press, Stanford, Calif. v - xiii + 3 - 502; 46 plts.

Robson, Elaine A.
1961. The swimming response and its pacemaker system in the anemone *Stomphia coccinea*. Journ. exp. Biol. 38: 685 - 694

Rosin, Ruth
1969. Escape response of the sea-anemone *Anthopleura nigrescens* (Verrill) to its predatory eolid nudibranch *Herviella* Baba, spec. nov. The Veliger 12 (1): 74 - 77 (1 July 1970)

Russell, Henry Drummond
1942. Observations on the feeding of *Aeolidia papillosa* L., with notes on the hatching of the veligers of *Cuthona amoena* A. & H. The Nautilus 55 (3): 80 - 82

Stehouwer, H.
1952. The preference of the slug *Aeolidia papillosa* (L.) for the sea anemone *Metridium senile* (L.) Arch. néerl. Zool. 10: 161 - 170

Swennen, Charles
1961. Data on distribution, reproduction and ecology of the nudibranchiate Mollusca occurring in the Netherlands. Netherl. Journ. Sea Res. 1 (1 - 2): 191 - 240

Wolter, Helma
1967. Beiträge zur Biologie, Histologie und Sinnesphysiologie (insbesondere der Chemorezeption) einiger Nudibranchier (Mollusca, Opisthobranchia) der Nordsee. Zeitschr. Morph. Ökol. Tiere 60: 275 to 337

Wood, Langley
1968. Physiological and ecological aspects of prey selection by the marine gastropod *Urosalpinx cinerea* (Prosobranchia: Muricidae). Malacologia 6 (3): 267 - 318 (30 June 1968)